

TORREYA

Vol. 38

July-August, 1938

No. 4

Rust Fungi in Norton, Massachusetts

MABEL A. RICE

Wheaton College, Norton, Massachusetts, lies in level country. Approaching by train from Boston one looks a regretful farewell to Blue Hill whose dome rises above a base line of swamp and wood. In compensation for this monotony the homesick botanist from the Berkshire Hills, fishing the swampy pools, finds a rich yield of pond scums; finally, she is almost content as the fields and woods prove a happy hunting-ground for rusts. These fungous parasites upon green plants are known to the world generally only through the wheat rust; and known there, perhaps, only as rusty, red or black spots on leaf and stem whereby the yield of the wheat grain is reduced. It is the seasons with over-wet harvests in which wheat rust especially flourishes. In the level, much-watered environs of Wheaton College a variety of rust parasites flourish.*

A certain botanist (35) explains that rusts "are dear to the botanical teacher because of their heterogeneously polymorphic ontogeny." For this reason, or for others which I will not pause to state, I have been pleased to find and to keep rusts as members of the Norton plant community. I report my findings in the list given below and proceed to add some words of introduction for those readers who would become acquainted with this plant community.

The list is in proper alphabetical order but I will take them as we meet them. First—on the campus the hollyhocks harbor a perennial rust. In a sheltered corner of a border against a brick building one may gather orange-flecked leaves in every month of the year. Even leaves dug from under a snow cover show orange pimples: spore clusters which in the spring will

* All of the rusts described as found near Norton are undoubtedly to be found in most regions where the same hosts grow, so may be looked for in the New York area. Editor.

break the leaf epidermis and be scattered upon new leaves to start an epidemic which, by midsummer, will have caused all the basal leaves of the hollyhocks to wither. This cosmopolitan has apparently colonized the world within the last century. Within the concise records of botanical journals, recording the occurrence of rust on plants of the mallow tribe, is hidden many a story of stow-away travel. (26) The earliest record proves it was growing in Chili in 1852. In 1857 it was reported on hollyhocks in Australia. The first record for Europe reports it in Spain in 1869. In 1873 it is reported from Bordeaux and Devonshire. By 1890 it had apparently colonized Europe and there is mention of it in Asia, Africa and the Canary Islands. In North American records the earliest date of its occurrence is 1888. (30) It evidently travelled westward. In 1905 it had not been found in Minnesota (33) but today it is found all over the United States. Many a gardener has come to accept yellowed leaves on the blossoming hollyhock spikes; the energetic gardener will need to give a weekly dusting of sulphur to his new plants if he will keep out the rust. (36) Even should this be effected at Wheaton we shall keep the rust in our community as the little round-leaved mallow, a weed of the campus green, is also host to the rust.

One needs microscopic mounts of cut leaves in order to see more of a rust plant than its fruit. The delicate, colorless strands of the fungus push their way between the cells of a leaf with a minimum of disturbance. They send only capillary branches through the cell walls and then, in contact with the living host cell, enlarge into swollen tips for feeding. These short branches, within the cell wall, but within the protoplasm only in the sense in which an ingested food particle is within an amoeba, are called haustoria. (49) By means of these the rust invader feeds without killing the host cells. The invaded cell is host perforce but the rust parasite feeds and drinks with a restraint which preserves the source of supply until, as the demands of fruiting time overcome the habits of restraint in the rust, water and sugar become scarce for two. Even then the drain upon the host is evident chiefly in the gradual drying out of the infected areas. It follows naturally upon these feeding habits of the rust parasite that a healthy plant is preferred as host: a reversal of the old dictum that the weakling is the natural prey to disease. (48)

The old Greek term, parasite, has undergone shifts in meaning since it was coined. Stripped of the connotation, flattery, it gives a graphic picture of the rust fungus which literally sits "beside the food" in the cells of a green plant. The rust fungus will take its food only from a living cell. Therefore rusts may not be grown on dead culture media in the laboratory as are bacteria. (43)

In the case of hollyhock rust a special interest attaches to the haustoria. The Swedish botanist, Jakob Eriksson, published studies of rust-infected hollyhock leaves in support of his "Mycoplasm Theory." (26) Eriksson was an authority upon cereal rusts and he formulated, in 1897, the "Mycoplasm Theory" to explain epidemics of grain rusts which he thought the rust spores alone were unable to initiate. (23) He described a formless fungous substance within the substance of the living host cells which he believed was handed on in dormant state from cell to cell of a growing plant, and from plant to seed. He figured these "internal germs" or "corpuscles speciaux" developing into definitely outlined spheres, lengthening into filamentous form within the host cells, penetrating the wall by capillary hyphae, finally developing a wealth of hyphae between the host cells—in short becoming the well known intercellular fungus which produces the eruption of spores upon the leaf surfaces. Marshall Ward in 1903 proved by a series of convincing drawings of infected grass tissue that Eriksson had reversed the story of rust development from a spore; that the "corpuscles" in cells of the leaf sections were merely the cut ends of haustoria; that the stalked filaments were not leaving the cells but were haustoria which had entered the cells for absorption purposes. (62) It is hard, however, to convince the originator of the fallacy of a pet theory. In 1904 and 1905 Eriksson again figured his "mycoplasm" in elaborate and accurate drawings of sections of rusted grain leaves: drawings which need only the addition of arrows of reverse direction to fit the accepted interpretation. (25) In 1911, still in elaboration of his theory, he published the afore-mentioned monograph upon the hollyhock rust; (26) also in 1917 and 1918 he figured the "mycoplasm" in another fungus, mildew of potato. (27) An Englishman again undertook a refutation. In 1920 Bailey chose the mallow rust for culture experiments. He took seeds

from rusted plants and, by growing them in sterile globes, proved that the rust was not transmitted through the seed. (13) Nevertheless, in 1930, the year before Eriksson's death, in his second edition of *Fungous Diseases of Plants*, "mycoplasma" is described in the case of a variety of fungi, including hollyhock rust. (28) The theory is interesting as possibly a lingering trace of an earlier idea that fungi were a lower order of plant life spontaneously evolved by a diseased plant. (48)

Today, with the "Mycoplasma Theory" tabled, hollyhock rust still offers problems to the botanists. While rusts as a tribe specialize in different spore forms in order the better to keep in connection with their hosts, hollyhock rust bears only teleuto-spores. The story of its development is not yet fully told. Rusted hollyhock leaves offer their abundance for the problems. (3, 4)

Gardening and rust collecting are incompatible pursuits. This fact is brought home to me when one of the students in horticulture suggests cutting off and burning the "cedar apples" which prove the presence of rust infection in the red cedar trees in front of the library. Cut them off, and I should have to go farther afield to demonstrate rust galls to a class; or to watch the hard, brown balls take on the appearance of orange-colored chrysanthemums when, on some rainy day in May, the spores push out in gelatinous ribbons. Red cedar flourishes in the sandy environs of Norton and the coming of these orange, fungous balls on the dark trees along the country roads is, to the initiated, one of the annual spring events.

These spores, like those of the hollyhock rust, are teleuto-spores: "final spores" in the life cycle: but cedar rust is a plant of more diverse habits than the hollyhock rust. The spores require a change of host; they will produce infection only upon apple leaves. On the apple leaves the parasite ripens two other forms of spores: spermatia which ooze out on the leaf surface in tiny drops of nectar, and aecidiospores which form in little "cluster cups," aecidia. The latter spores carry infection back to the cedars and complete an interesting even though a vicious cycle. Thus the name of this rust is properly cedar-apple rust although the term, "cedar apple," has come to be applied to the galls upon the cedar trees. The apple host seems to fare worse than the cedar. Perhaps the shorter life term of the spring generation

requires heavier feeding. At any rate the thickened, infected leaf areas lose their chlorophyll and the sugar-forming power of the tree must be much reduced. Our infected Bechtal crab shows poor health by its lessened flowering and its winter-killed branches. The apple rust lives for only one season but it is apt to recur annually in this region of abundant cedars. Their abundance makes the extermination of the cedar link impracticable; the apple growers instead must hunt for immune varieties of apple or keep busy with sprays. (20)

Red cedar is host to some twelve different species of the rust, *Gymnosporangium*. (9) Four of these occur in New England and I am chagrined to have found only two in Norton. The bird's-nest rust, *Gymnosporangium nidus-avis*, causes more disturbance to its host than does the cedar-apple rust, *Gymnosporangium juniperi-virginianae*. Not only do the leaves of infected branches develop the needle-shaped form characteristic of a seedling tree, an effect caused also by the apple-cedar rust, but the growth of the main axis is checked and the branches grow in a dense cluster: the "bird's-nest." (58) Red cedar is hardy stock. I have found it holding its own against these two parasites . . . with gay "cedar apples" on its green branches while half-dead "bird's-nest" clusters distort other branches. On these latter, gelatinous masses of teleutospores ooze out, in the spring, from cracks in the bark.

Around Norton shad bush is the most frequent alternate host for the bird's-nest rust. Both leaves and fruit show annually a heavy eruption of spermatia and aecidiospores. Shad bush is also alternate host to another *Gymnosporangium* of the Norton group: *Gymnosporangium clavariaeforme* which infects the prickly dwarf cedar or juniper. (58) Plants which were moved from the fields to the campus rock-garden develop each spring the characteristic masses of yellow teleutospores along the branches. Again the pathologist downs the gardener and keeps the rather scraggy juniper as a prized exhibit.

This is, indeed, a small list of *Gymnosporangiums* for Norton. I reflect regretfully upon time spent in the laboratory instead of in the field. We have white cedar as well as red cedar, and sweetfern in abundance but I have never found the white cedar rust which, unlike its thirty sister species, chooses sweetfern for its alternate host instead of one of the apple tribe. (34)

The proof of this alternation between white cedar and sweetfern as hosts for the rust, *Gymnosporangium Ellisi* was made in Arthur's laboratory at Purdue. (10) This is but one of many determinations of doubles in the rust world made since de Bary showed the way in 1865 by germinating teleutospores of wheat rust upon leaves of barberry and vice versa. (14) In this connection an amusing bit of ancient history in botany is recorded in the Gardener's Chronicle of 1867. An Englishman named Smith expresses doubt concerning the German de Bary's conclusions. He writes: . . . "If any botanist will cause an Aecidium-spore . . . to germinate on corn . . . and produce from its mycelial thread a Uredo-spore . . . the case will be proved, i.e., if the said botanist can permanently preserve his specimen on a microscopic slide, and send it to the British Museum for all comers to examine." (55) It may be noted that in Europe the term, corn, means any cereal except maize.

The barberry is allowed to rust undisturbed in the Wheaton Pines since wheat is not a commercial crop in this region. Two other grains also furnish us rust. Each fall college opens in time for us to find rust on leaves of late-standing corn. On the leaves of these dying corn stalks it is possible to find many examples of the "green island" phenomenon. (43) Even when the leaves are dry and yellow the infected area around each rust pustule is green. The fungus seems to serve as a water reservoir and, as the host plant ages, longer life is given the infected cells than those of the rest of the leaf. (49) The corn leaves bear both the brown pustules of uredospores which spread the infection on corn all summer and the black teleutospores which, after overwintering, can complete the rust cycle on the yellow-flowered Oxalis of our fields. This is another of the cycles established by Arthur (8) and although rust on Oxalis is of rare occurrence in the field it is easy to make the shift on Oxalis weeds in the planthouse. The overwintering which the teleutospores require may be effected in the ice-chest. One fall the class had the further good fortune to find crown rust of oats, so called because the thickened tip of each yellow teleutospore suggests a crown. The oats had been harvested but, judging from the condition of the volunteer tufts which had escaped the sickle, the crop must have been heavily rusted. That field has not again been planted to oats. I never learned whether the

farmer gave it up because he found out the significance of a hedge of buckthorn just across the road. On this hedge and on buckthorn in the college woods one may find, each May, the alternate stage of the oat rust.

These grain rusts are of special interest because the records of their occurrence carry us back to the beginnings of knowledge about rust fungi. The Romans called rust *Rubigo* and worshipped the god *Rubigo* each April as a protection against rust. The name is perpetuated in the name of one of the wheat rusts, *Puccinia rubigovera*. (11) By the help of the microscopes of the eighteenth century rusts were recognized as plants and called fungi. The Italian, Fontana, in 1767, made a very creditable drawing of spores of wheat rust and states that they "are very minute plants that nourish themselves at the expense of the grain." Fontana was an enthusiast over microscopic study and recommends more looking and less theorizing: "The talents of many learned botanists could be used to greater advantage in the little-known fields of the vegetable kingdom, if, instead of furiously pursuing new systems and enriching with new barbarous words one of the most delightful and perhaps the most useful branches of the science of nature, they observed the structure of plants more closely . . .". (31) Perhaps because men did not follow this advice, gross misconceptions about the nature of rust fungi persisted until de Bary, by his researches, made a real science of the study of fungi. (11)

At first no different species of the grain rust were distinguished but gradually it became clear that the grain rusts are strict specialists, that wheat rust will not infect oats, nor the reciprocal. As the facts stand today the story is even more amazing. The same Jakob Eriksson whose "Mycoplasm Theory" botanists did not accept is recognized as pioneer in the work of distinguishing "form species" of the cereal rusts: forms which look alike, which can be distinguished only "in that every form is almost exclusively confined to its particular cereal and that consequently it is able to infect no other cereal but that one." (24) Before 1890, Eriksson states, only three species of grain rust were recognized: one on oats, one on wheat and rye, and one, *Puccinia graminis* which was thought to be able to infect all the cereals and many species of wild grasses. By 1898 Eriksson had differentiated ten distinct forms of rust

on the four cereals. (24) An American has been foremost in continuing this work with *Puccinia graminis*. In 1926 Stakman distinguished some fifty "physiologic forms" of *Puccinia graminis tritici* in the United States. (57) Work of the last ten years has raised the number to nearly one hundred fifty. These results are the outcome of an attempt to breed rust-resistant varieties of wheat. (29) It will be readily seen that this great number of biologic species of the rust has added difficulties to the solution of that problem.

Rust-resistant varieties have been much more successfully produced against the less highly specialized asparagus rust which we find in Norton on roadside escapes from gardens. The development of a resistant asparagus was the work of the United States Department of Agriculture in cooperation with the Massachusetts Agricultural Experiment Station. Asparagus varieties from all parts of the world were grown at Concord, Massachusetts. A cross between English and American strains produced the now world-famous Washington strains. (59, 60) Agricultural handbooks now advise the control of asparagus rust by the planting of rust-resistant strains; gardener's catalogues list Martha and Mary Washington asparagus.

Asparagus rust was described by de Candolle in 1805 (16) but the first record of its occurrence in America was in a report by Halsted in 1896 of a rust epidemic in New Jersey, Delaware, Long Island and New England. (38) This destruction of the eastern crop gave California a chance to develop the asparagus culture but the rust travelled westward and in seven years had reached California. The rust produces all spore forms on the one host but the summer uredospores are thought to be chiefly responsible for the spread of infection. Blown by moist winds they could colonize nearby fields, and so, slowly but independently, travel across the continent. The picture is graphically drawn by R. E. Smith. "When one sees the cloud of dust which arises from rust plants when disturbed, coloring . . . anything passing through the field a deep red color, flying away in the wind like smoke, covering the berries which contain the seed, covering and coloring the ground from which roots are dug for sale, and reflects that each minute particle of this dust is a rust spore, it would seem that the spread of the disease must occur in many ways through the agency of these summer spores.

Practically, however, there appears to be but one mode of distribution at all common, which is the distribution of uredospores by the wind." (54)

I have called asparagus rust a less highly specialized parasite. Evidence of this is seen in its lesser adjustment to life with its host. It is definitely toxic in its effect upon the invaded cells. The leaves of an infected plant soon fall. The plant thus loses the power of building food for next season's growth and the asparagus stock is weakened. In striking contrast to the asparagus is the rust of *Pyrola*, the little shin-leaf of our woods. Here is restraint in feeding and an almost entire absence of toxic action by the rust parasite which makes it likely that rusted *Pyrola* will long continue resident in the Wheaton Pines. All through the twenty-five acres of wooded land which adjoin the campus grow scattered patches of shin-leaf. The shining, evergreen leaves make a pleasing contrast to the ground cover. By the end of March, sometimes when the snow has barely gone, another color note is added for in many of the patches the under surface of each leaf is covered with an eruption of orange-colored spores. A week or two later pustules of the paler yellow teleutospores may, by aid of a hand lens, be distinguished among the uredospores. These teleutospores germinate while still on the *Pyrola* leaf and their secondary spores carry infection to spruce trees. Scales of young cones are said to be particularly susceptible. This spruce rust is well known in northern forests but I have never found it here. (32) The *Pyrola* rust apparently thrives without its alternate host. It lives as a perennial in the rootstock of its perennial host and each spring the abundant uredospores can infect other *Pyrola* plants. There are many perennial rusts but our interest in this one centers upon the long vegetative period of the fungus. It does not fruit on the young spring leaves but comes to fruition the following spring on the overwintered leaves. These wither normally in May as new leaves develop and the rust whose pustules have broken the under epidermis seems to make little difference in the time of their withering. (52)

Hepatica rust is companion in the spring to *Pyrola* rust but with a different sequence. *Hepatica* plants are not found in Norton but I have transplanted them from the Berkshire Hills to our Botanic Garden. The rust came with them and each

spring certain plants send up rusted leaves as their first growth. The leaves are punctate first with tiny, sticky spermogonia; then between the spermogonia there develop the flower-like cluster-cups of aecidiospores. Even with the heavy spore production the leaves remain green but there is sufficient toxic action to stimulate greater growth with abnormal results. The leaves are smooth instead of downy, the blades are reduced in size and stand stiffly erect on long petioles. Blossoms are few on an infected plant; instead of blossoms a set of normal leaves follows the rusted ones; the rusted ones die off by the end of May and the rust, hidden in the rootstock, is seen no more until next spring. (52) I have watched the recurrence of rust on these same plants for half a dozen years but there has been no infection of the other Hepaticas. The aecidiospores need an alternate host, the plum or cherry for their growth. I have made this cross infection in the planthouse but I allow neither plum nor cherry near my bank of Hepaticas.

It is intriguing, although perhaps futile, to speculate over the choice of hosts by these rusts which require a change of host for the completion of their life cycles. A chance wind may explain the transfer of spores but there seems, in the dissimilar hosts, no common character by which to explain such limitations. (40) The contrast in hosts is particularly striking in the case of the rusts of coniferous trees. Aecidiospores from rust on the larch infect willow. When we explore the shores of the Reservoir, left dry in the autumn, we find the willow leaves peppered with yellow clusters of teleutospores for the larch. The seemingly wayward fancies of the cedar rusts have been mentioned. The spruce rust at least chooses a perennial evergreen from among the herbs at its base. The blister rust of the white pine, however, jumps to currant and gooseberry for its teleutosporic stage.

Here is another immigrant from Europe. In 1906 it was found in a plantation of white pine seedlings which had been imported from Germany; at about the same date it was found on imported white pine seedlings in other New England states and in New York. Its eradication has now become a forestry problem. The government, in an attempt to save the valuable white pine, has undertaken to eradicate the currant tribe, the lesser host. With the currant link removed, an infected pine

tree is not a menace in a community but the tree is doomed once the main trunk is invaded. We hope that pruning has saved the one or two infected pines of this vicinity. Infection is most generally through the leaves or the bases of the leaf clusters. In mature trees it may be some years before the cambium, the growing layer of the trunk, is reached and killed by the fungus but seedling trees are quickly girdled and killed. (18)

The pitch pine is host to several rusts, each one with a different alternate host. From New Jersey southward there is a species which shifts to oak. Around Norton in May, I have found on needles of the pitch pine the tiny projections of aecidia of *Peridermium acicolum*. In the fall any clump of goldenrod may show the bright yellow clusters of its uredo and teleutospores on the under-leaf surfaces. (45) In the fall also one finds on leaves of sweetfern the slender, brown, hair-like clusters of teleutospores of *Peridermium comptoniae*. The aecidial stage of this rust deforms the pitch pine host; it causes a fusiform swelling of the main stem of young trees. (56)

These tree rusts have taken us far afield but if we walk again through college grounds we may add to our list two more rusts of double hosts. In May the elder bushes are in full foliage and both leaves and stems are swollen with a rust infection. Arthur in 1902 linked the elder rust with a teleutosporic stage on one of the sedges. His description of his preliminary guesses and his methods of verification give incidentally a glimpse of a man with an absorbing interest. (7)

The fields in May are whitened by blossoming *Houstonias*. At close range one may distinguish among them clumps where the flowers stand taller than their neighbors and where the leaves have lost all green color. Such plants are found to be literally covered with eruptions of spermatia and aecidia; even the calyx of the flowers shows the infection. The rust here has much the same effect as has the absence of light upon plants. Lacking light a plant does not build chlorophyll and therefore cannot build sugars. The botanist calls this condition etiolation and explains: "An etiolated plant is growing to death at the expense of what organic carbon compounds it possessed at the beginning." (6) In the case of the rusted *Houstonias* the parasite is the cause of the etiolation yet in other respects this parasite shows the usual restraint and adaptation of a rust to

its host. Under microscopic examination the infected cells show no abnormal effects other than lack of chlorophyll. The *Houstonia* rust shifts to another meadow plant. Blue-eyed grass, a neighbor in the fields, is the teleutosporic host. (53) A summer resident should certainly find it in Norton.

Rust of carnations, although of greenhouse cultivation, stands in our list since we find it frequently in nearby greenhouses. This cosmopolitan rust, a pest to carnation growers, came from Europe and seems to have left behind its aecidial host. (37) Indeed its claim to heteroecism (14) rests merely upon the reports of a few cross inoculations from *Euphorbia geradiana* to the carnation. (12) Both in Europe and America the rust continues upon the carnation by means of its repeating spores, the uredospores. For a fungus which can pass the winter under glass no other spore form, and no alternate host is necessary.

There are several single-host rusts at Wheaton. Hollyhock rust which we met at the start is one, and asparagus rust. *Potentilla* rust is another. As the March sun strikes along the foundations of our brick buildings flecks of orange appear on the green rosettes of the "five-finger" *Potentilla*. By April the uredospores are so abundant that patches of *Potentilla* in the turf near the rock garden seem touched with orange paint. Uredospores of this rust act like aecidiospores in that a cell fusion which precedes their formation gives them double nuclei. (17) Here is introduced the fascinating, unsettled question of sexual reproduction in the rusts. Structures which produce egg cells have not been found in rust fungi. When in certain rusts a fusion between cells (17) or in others a migration of a nucleus into a cell at the base of an aecidium was discovered (15), rusts were treated as examples of plants where a substitute fusion had taken the place of fusion between sexual cells developed on sexual structures. When Craige took his cue from the chance fly in the planthouse and mixed the drops of spermatogonial fluid upon a rust-infected barberry leaf he discovered that spermatia function in producing aecidiospores. (19) This discovery that the spermatia, long considered functionless spores, have a part to play in reproduction has renewed the interest of botanists in bean rust (5, 6), in wheat rust on the barberry (1, 2), in corn rust on *Oxalis* (50), in all spermatogonial-aecidial rust stages . . . but a discussion of this problem would

keep us too long away from our campus wanderings. Rust of violets is good material for work upon reproduction (50) and Wheaton has an abundant supply. *Viola fimbriatula* blooms in April and along with its deep blue blossoms the spermatia and aecidiospores of rust make gay yellow spots on its leaves. The familiar, long-stemmed, blue violet follows with plenty of rust. Although building alterations destroyed a choice plot there are still rusted specimens in the rock garden. The little white violet of the woods is also host to the rust. It is upon leaves of this white violet that we are most apt to find the black teleutospore clusters in the fall. Thus we complete the cycle of violet rust.

In May a rust appears wherever dewberry trails over fields, across footpaths, or along roadsides. Its unfolding leaves are covered with a crust or caeoma of aecidiospores. This rust, *Caeoma nitens*, introduces still another problem. Its aecidiospores should reinfect dewberry and later, teleutospores from that generation should complete the cycle. Kunkel in a series of germination studies, where he watched under the microscope the germination of spores in drops of various nutrients, discovered that some of the aecidiospores of *Caeoma nitens* acted like teleutospores. These spores sent out a four-celled filament and formed the characteristic four spores by which a teleutospore starts a new rust generation. (41) Here is seen the scientist's "deep insatiable curiosity about the things of nature." (39) Kunkel examined spores of *Caeoma nitens* gathered from New Hampshire to Virginia and discovered a short-cycle and a long-cycle race. The decisive character is the habit of the germinating aecidiospores but he found also a slight difference in size and shape of the spores and a color difference. The spores of the short-cycle race match Cadmium orange; those of the long-cycle, Xanthine yellow. One may check ones color-sensitiveness to yellows by matching leaves of rusted dewberry and then verify the rust strain by sowing the spores in drops of water and watching their germination. There is, of course, a phylological interest here. Which is the primitive race? Kunkel thinks the short-cycle one the primitive and the one with an extra spore form the derivative. (42) *Caeoma nitens* is apparently trying out experiments. Pady reports that in new infections of blackberry canes the rust grows through the host cells instead of between the cells as is usual for a rust. It develops

coiled branches within the cells; only after about the tenth day of an infection are these gradually replaced by intercellular runners with haustoria. This is evidently a device to further the quick establishment of the fungus in its host. (46)

Another rust, *Kuehneola albida*, infects the blackberry but this one we find in the fall. We prize it then for we can get a class exhibit as long as the reddened blackberry leaves hang on the canes. Clover rust is also on the campus late in the fall. We find it on both the white and the red clover. There is a nice problem here in distinguishing the form-species of *Uromyces trifolii*. (44) Snapdragons in the President's garden can usually be depended upon to give us samples of rust until frost kills the host. Snapdragon rust has reversed the usual course of emigration. It was reported in California in 1895 and by 1915 had colonized New England both in greenhouses and in out-of-door gardens. The rust perpetuates itself by means of the abundant uredospores; its teleutospores apparently do not germinate. As is the case with the carnation rust, teleutospores "are not a necessity for a fungus the host of which occurs both under glass and out of doors." (21)

Several of the rusts on native plants take kindly to plant-house culture. *Chrysomyxa cassandrae* was discovered in mid-winter on a plant of leather-leaf which had been brought in for forcing in a terrarium. Dandelion rosettes brought into the planthouse bloom and fruit in the winter. We have even raised a crop of seedling dandelion and have raised rust upon them: a chance infection from a rusted rosette. The rust of Jack-in-the-pulpit can be forced along with its host. The stage which bears spermatia and aecidiospores is perennial in its host. It is wise to locate the rusted plants in the woods when these spores cover leaves and spathes in May if one would find the underground corms for transplanting in the fall, for by that time the leaves are dead and the late spores, the teleutospores, are scattered in the soil where they may infect new shoots as they push up in the spring. We do not need this late stage for the planthouse; we have only to dig the labelled corms and in February, in our terrarium watch the rust pustules appear even before the Jack leaves unfold.

This adaptable rust seems an interesting plant rather than a disease-producing fungus. Without attempting to minimize

the loss to agriculture from rusted grain, or to our forests from rusted pine, nevertheless, under the microscope a rust-invaded plant cell shows us a very delicate interrelation between host and parasite. I have even on occasion taken up literary cudgels in defense of Jack-in-the-pulpit rust when it has been used as an example of a toxic parasite. (22, 51) The development of mutualism is an interesting matter. It is chief among those other reasons because of which I welcome these twenty-six rusts as members of the Norton plant community.

<i>Rust</i>	<i>Host</i>
1. <i>Aecidium punctatum</i> Pers.	<i>Hepatica acutiloba</i> DC.
2. <i>Aecidium sambuci</i> Schw.	<i>Sambucus canadensis</i> L.
3. <i>Caeoma nitens</i> Burrill	<i>Rubus villosus</i> Ait.
4. <i>Chrysomyxa cassandrae</i> Tranz.	<i>Chamaedaphne calyculata</i> (L.) Moench.
5. <i>Chrysomyxa pyrolae</i> Rostr.	<i>Pyrola americana</i> Sweet.
6. <i>Cronartium ribicola</i> F. de Waldh.	<i>Pinus Strobus</i> L.
7. <i>Gymnosporangium clavariaeforme</i> DC.	<i>Juniperus communis</i> L. & <i>Amelanchier oblongifolia</i> (T. & G.) Roem.
8. <i>Gymnosporangium juniperi-virginianae</i> Schw.	<i>Juniperus virginiana</i> L. & <i>Malus</i> sp.
9. <i>Gymnosporangium nidus-avis</i> Thaxter	<i>Juniperus virginiana</i> L. & <i>Amelanchier oblongifolia</i> (T. & G.) Roem.
10. <i>Kuehneola albida</i> Magnus	<i>Rubus</i> sp.
11. <i>Melampsora Bigelowii</i> Thüm.	<i>Salix</i> sp.
12. <i>Peridermium acicolum</i> Underw. & Earle	<i>Pinus rigida</i> Mill. & <i>Solidago</i> sp.
13. <i>Peridermium comptoniae</i> Orton & Adams	<i>Myrica asplenifolia</i> L.
14. <i>Phragmidium potentillae-canadensis</i> Diet.	<i>Potentilla canadensis</i> L.
15. <i>Puccinia antirrhini</i> Dietel & Holway	<i>Antirrhinum</i> sp.
16. <i>Puccinia asparagi</i> DC.	<i>Asparagus officinalis</i> L.
17. <i>Puccinia coronata</i> Corda	<i>Avena</i> sp.
18. <i>Puccinia graminis</i> Pers.	<i>Berberis canadensis</i> Mill.
19. <i>Puccinia malvacearum</i> Mont.	<i>Althaea rosea</i> Cav. & <i>Malva rotundifolia</i> L.
20. <i>Puccinia sorghi</i> Schw.	<i>Zea Mays</i> L.
21. <i>Puccinia taraxaci</i> Plowr.	<i>Taraxacum officinale</i> Weber
22. <i>Puccinia violae</i> DC.	<i>Viola</i> sp.
23. <i>Uromyces caryophyllinus</i> Wint.	<i>Dianthus caryophyllus</i> L.
24. <i>Uromyces caladii</i> Farl.	<i>Arisaema triphyllum</i> (L.) Schott.
25. <i>Uromyces houstoniatus</i> J. Sheldon	<i>Houstonia caerulea</i> L.
26. <i>Uromyces trifolii</i> Lev.	<i>Trifolium</i> sp.

Literature cited

1. Allen, Ruth F. 1930. A cytological study of heterothallism in *Puccinia graminis*. Jour. Agr. Res. 40: 585-614. pl. 1-17.
2. ———. 1933. Further cytological studies of heterothallism in *Puccinia graminis*. Jour. Agr. Res. 47: 1-15. pl. 1-6.
3. ———. 1933. A cytological study of the teliospores, promycelia and sporidia in *Puccinia malvacearum*. Phytopath. 23: 572-586. f. 1-4.
4. ———. 1935. A cytological study of *Puccinia malvacearum* from sporidium to the teliospore. Jour. Agr. Res. 51: 801-818. pl. 1-9.
5. Andrus, C. F. 1931. The mechanism of sex in *Uromyces appendiculatus* and *Uromyces vignae*. Jour. Agr. Res. 42: 559-587. f. 1-11.
6. ———. 1933. Sex and accessory cell fusions in the Uredineae. Jour. Wash. Acad. Sci. 23: 544-557. f. 1-3.
7. Arthur, J. C. 1902. Clues to relationship among heteroecious plant rusts. Bot. Gaz. 33: 62-66.
8. ———. 1904. The acididium of maize rust. Bot. Gaz. 38: 64-67.
9. ———. 1907. No. Amer. Flora. 7, pt. 2: 83-969.
10. ———. 1921. Nineteen years of culture work. Myc. 13: 1899-1917.
11. ———. 1929. The plant rusts. 1-446. f. 1-186. New York. John Wiley & Sons.
12. ———. 1934. Manual of the rusts in United States and Canada. 1-438. f. 1-463. Lafayette, Ind. Purdue Res. Found.
13. Bailey, M. A. 1920. *Puccinia malvacearum* and the mycoplasma theory. Ann. Bot. 34: 173-200. f. 1, 2.
14. Bary, A. de. 1865. Neue Untersuchungen über Uredineen. Monatsber. k. Preuss. Akad. Wiss. Berlin. 15-50. pl. 1.
15. Blackman, V. H. 1904. On the fertilization, alternation of generations and general cytology of the Uredineae. Ann. Bot. 18: 323-373. pl. 21-24.
16. Candolle, A. P. de. 1805. Flore française. 3rd. ed. 2: 1-600. Paris, H. Agasse; Desray.
17. Christman, A. H. 1907. The nature and development of the primary uredospore. Trans. Wis. Acad. Sci., Arts and Letters. 15, pt. 2: 517-524. pl. 29.
18. Clinton, G. P. & McCormick, F. A. 1916. Infection experiments of *Pinus Strobus* with *Cronartium ribicola*. Conn. Agr. Exp. Sta. Bull. 214: 428-459. pl. 37-44.
19. Craigie, J. H. 1927. Discovery of the function of the pycnia of the rust fungi. Nature 120: 765-767. f. 1, 2.
20. Crowell, I. H. 1934. The hosts, life-history and control of the cedar-apple rust fungus *Gymnosporangium juniperi-virginianae* Schw. Jour. Arnold Arboretum. 15 (3): 163-232. pl. 1-8. +f. 1, 2.
21. Doran, W. L. 1921. Rust of *Antirrhinum*. Mass. Agr. Expt. Sta. Bull. 202: 39-66. pl. 1, 2.
22. Dufrenoy, J. 1929. L'étude cytologique des rapports entre parasite et cellule-végétale. Ann. Inst. Pasteur. 43: 218-222. f. 1-4.
23. Eriksson, Jakob. 1897. Vie latente et plasmatique de certaines Urédinées. Comptus Rendus. 124: 475-477.

24. ———. 1898. A general review of the principal results of Swedish research into grain rust. *Bot. Gaz.* 25: 26–38.
25. ———. 1904, 1905. Über das vegetative Leben der Getreiderostpilze. *K. Sv. Vet.-Akad. Handl. Bd.* 38: 1–18. pl. 1–3. Bd. 39: 1–40. pl. 1, 2.
26. ———. 1911. Der Malvenrost. *K. Sv. Vet.-Akad. Handl. Bd.* 47: 1–125. pl. 1–6+f. 1–18.
27. ———. 1917, 1918. Développement primaire de mildiou (*Phytophthora infestans*) au cours de la végétation de la Pomme de terre. *Revue Générale de Botanique.* Tome 29: 257–260; Tome 30: 16–61. pl. 1–13.
28. ———. 1930. *Fungous diseases of plants.* 2nd. ed. trans. Wm. Goodwin. London. Baillière, Tindall & Cox. 1–526. f. 1–399.
29. Ezekiel, W. N. 1930. Studies on the nature of physiologic resistance to *Puccinia graminis tritici*. *Univ. Minn. Agr. Exp. Sta. Bull.* 67: 1–62. f. 1–11.
30. Farlow, W. G. & Seymour, A. B. 1888. A provisional host-index of the fungi of the United States. pt. 1: 1–51. Cambridge.
31. Fontana, Felice. 1767. trans. Pirone, P. P. 1–40. pl. 1. Washington. Hayworth Printing Co. 1932.
32. Fraser, W. P. 1911. Cultures of some heteroecious rusts. *Mycologia* 3: 67–74.
33. Freeman, E. M. 1905. Minnesota plant diseases, 1–432. f. 1–211. Rust of hollyhocks and mallows. *Bot. Ser. V:* 372, 373.
34. Frome, F. D. 1914. A new Gymnosporangial connection. *Mycologia* 6: 226–230.
35. Ganong, W. F. 1922. *The living plant.* 1–478. f. 1–178. New York. Henry Holt & Co.
36. Gregory, C. T. & Davis, J. J. 1928. *Common garden pests.* 1–150. ill. Des Moines, Iowa. Better Homes and Gardens.
37. Grove, W. B. 1913. *The British rust fungi.* 1–412. f. 1–290. Cambridge, Univ. Press.
38. Halsted, B. D. 1898. The asparagus rust; its treatment and natural enemies. *N. J. Agr. Expt. Sta. Bull.* 129: 1–20. pl. 1, 2+f. 1–5.
39. Harper, R. A. 1920. The stimulation of research after the war. *Science N.S.* 51: 473–478.
40. Jackson, H. S. 1931. Present evolutionary tendencies and the origin of life cycles in the Uredinales. *Mem. Torrey Bot. Club* 18: 1–108.
41. Kunkel, L. O. 1913. The production of a promycelium by the aecidiospores of *Caeoma nitens* Burrill. *Bull. Torrey Club.* 40: 361–366. f. 1, a–e.
42. ———. 1920. Further data on the orange-rusts of *Rubus*. *Jour. Agr. Res.* 19: 501–512. pl. D, 92–94.
43. Mains, E. B. 1917. The relation of some rusts to the physiology of their hosts. 4: 179–220. pl. 4, 5.
44. ———. 1936. Host specialization of *Uromyces trifolii*. *Mich. Acad. Sci., Arts and Letters.* 21: 129–134.
45. Orton, C. R. & Adams, J. F. 1914. Notes on *Peridermium* from Pennsylvania. *Phytopath.* 4: 23–26. pl. 3.
46. Pady, S. M. 1935. The role of intracellular mycelium in systemic infections of *Rubus* with the orange-rust. *Mycologia* 27: 618–637. f. 1–42.

47. Persoon, C. H. 1801. *Synopsis methodica fungorum*. 1-706. pl. 1-5. Göttingae, apud Henricum Dieterich.
48. Raines, M. A. 1922. Vegetative vigor of the host as a factor influencing susceptibility and resistance to certain rust diseases of the higher plants. *Am. Jour. Bot.* 9: 183-203; 215-238. pl. 11, 12.
49. Rice, M. A. 1927. The haustoria of certain rusts and the relation between host and pathogene. *Bull. Torrey Club*. 54: 63-153. pl. 1-9.
50. ———. 1933. Reproduction in the rusts. *Bull. Torrey Club* 60: 23-50. pl. 4-6.
51. ———. 1934. The relation of *Uromyces caladii* and other rusts to their hosts. *Bull. Torrey Club* 61: 155-162. pl. 6-8.
52. ———. 1936. The cytology of host-parasite relations. *Bot. Rev.* 1: 327-354. pl. 1.
53. Sheldon, J. L. 1906. A rare *Uromyces*. *Torreyia* 6: 249, 250.
54. Smith, R. E. 1905. Asparagus and asparagus rust in California. *Agr. Exp. Sta. Univ. Calif. Bull.* 165: 5-99. f. 1-46.
55. Smith, W. G. 1886. Corn mildew and barberry blight. *Gard. Chron. n.s.* 25: 309, 310. f. 58-60.
56. Spaulding, P. & Hansbrough, J. R. 1932. *Cronartium comptoniae*, the sweetfern blister rust of pitch pines. *U. S. Dept. Agr. Bull.* 217: 1-22. f. 1-5.
57. Stakman, E. C. 1926. Physiologic specialization. *Proc. Int. Congr. Plant. Sci. Ithaca*. 1312-1330. Menasha Wis., Geo. Banta Publ. Co. 1929.
58. Thaxter, Roland. 1891. The Connecticut species of *Gymnosporangium*. *Conn. Agr. Exp. Sta. Bull.* 107: 2-6.
59. Thompson, R. C. 1930. Asparagus culture. *U. S. Dept. Agr. Bull.* 1646: 1-24. f. 1-8.
60. Waite, M. B. 1925. Year Book *U. S. Dept. Agr.* 452-599. f. 202-293.
61. Ward, H. M. 1890. Croonian Lecture—On some relations between host and parasite in certain epidemic diseases of plants. *Proc. Roy. Soc. London* 47: 393-443. f. 1-16.
62. ———. 1903. On the histology of *Uredo dispersa*, Erikss. and the "Mycoplasm" hypothesis. *Phil Trans. Roy. Soc. London. Ser. B.* 196: 29-46. pl. 4-6.

WHEATON COLLEGE
NORTON, MASS.